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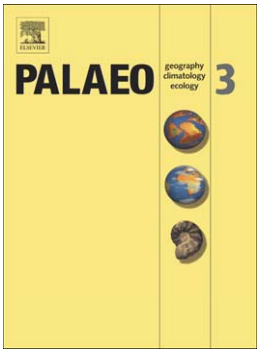

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High-resolution biochronology and diversity dynamics of the Early Triassic ammonoid recovery: the Dienerian faunas of the Northern Indian Margin

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Abstract

A new high resolution biozonation based on the Unitary Association (UA) method is constructed for the Dienerian ammonoid succession of the Northern Indian Margin. It includes 12 UA-zones and leads to the subdivision of the Dienerian into three parts (early, middle and late). The corresponding diversity analyses, coupled with results previously obtained for the early Smithian ammonoids of the same regions, highlight the four following phases: (1) a first modest peak of diversity in the early

Dienerian; (2) a very low diversity persisting throughout the middle Dienerian; (3) a slow increase of diversity during the late Dienerian, and (4) a marked diversification in the early Smithian. Turnover rates are very high during this entire time interval, and the boundaries between early-middle and middle-late Dienerian are emphasized by complete renewals of the ammonoid faunas. The low diversity values in the middle and early late Dienerian are concomitant with an anoxic event on outer continental shelves and coincide with warmer temperatures than those of the early Dienerian and early Smithian. This diversity pattern stands in strong contrast with the credo of a protracted or stepwise recovery following the end-Permian mass extinction. Together with the end-Smithian extinction, the middle and early late Dienerian diversity crises were likely both radical setbacks in the recovery of Early Triassic ammonoids. However, these two diversity crises do not necessarily imply identical environmental triggers that ultimately led to anoxic bottom waters on outer continental platforms in both cases.

1. Introduction

Modes and rates of biotic recovery following the end-Permian mass extinction are currently attracting a lot of efforts. Ammonoids have been documented to be one of the fastest clades to recover and even to largely overshoot their previous Permian record highs (Brayard et al., 2009). At the genus level, ammonoids show a low diversity in the Griesbachian, a slight increase during the Dienerian and an explosive radiation in the early Smithian (Brayard et al., 2006, 2009). Such a pattern provides the general outline of diversity trends, but is also influenced by uneven taxonomical practices across authors, relatively coarse time bins and the absence of consensus about some stage and sub-stage boundaries (i.e. Induan-Olenekian ill defined boundary; Brühwiler at al., 2010a). More recently, a significant advance toward a refined diversity analysis (Brühwiler et al., 2010b) hinged on a new, highly resolved biozonation of the Smithian from the Northern Indian Margin (NIM).

The NIM has long been recognised as a key area for the establishment of the Early Triassic time scale (Jenks et al., 2015). The Salt Range (Pakistan) and Spiti District (Northern India; Fig. 1) are especially notorious for their abundant and well preserved ammonoid faunas since the pioneer works of Waagen (1895) in the Salt Range and of Diener (1897) and Krafft & Diener (1909) in Spiti. However, until recently, no thorough and modern revisions of the taxonomy and biostratigraphy of the ammonoids of these two regions have been published. The understanding of most taxa described in these pioneering works is hampered by the small sample sizes and their approximate stratigraphic positions. Following the revision of the Smithian ammonoids from the Salt Range (Brühwiler et al., 2012a) and Spiti district (Brühwiler et al., 2012b), new abundant and well-preserved material allowed us to thoroughly revise the taxonomy and biostratigraphy of the Dienerian ammonoids from these two basins (Ware et al., submitted-a & b). As for the Smithian, they represent the most complete and detailed Dienerian ammonoid records known worldwide, with 12 Dienerian local maximal horizons in the Salt Range and 10 in Spiti, compared to only four horizons in Canada (Tozer, 1994), three in South Primorye (Shigeta et al., 2009) and four in Siberia (Dagys and Ermakova, 1996).

Here we present a new high-resolution ammonoid zonation for the Dienerian of the NIM based on a synthetic biochronological analysis of the Salt Range and Spiti basins at the species level. This new biostratigraphic scheme is based on bed by bed extensive collections in order to produce a reliable taxonomy reflecting intraspecific variation as well as the best possible resolution in time. Correlation of the Dienerian ammonoid succession of the NIM with other regions will need additional, similarly detailed work. Possible correlations are discussed in Ware et al. (submitted-a). This succession of the NIM provides a robust reference scheme for Dienerian times and further correlations at larger geographical scales. The hitherto poorly know Dienerian faunas can now contribute to an improved understanding of the Early Triassic recovery. The new highly resolved biostratigraphic framework allows the analysis of the biodiversity dynamics of the Dienerian ammonoids from the NIM with unprecedented detail, and to compare it with palaeoenvironmental proxies obtained from the same sections.

2. Material and methods

The method used here is the same as in Brühwiler et al. (2010b). Hence, only a short description is provided. The reader is referred to Brühwiler et al. (2010b) for further details. The new Dienerian biostratigraphic framework and ammonoid diversity data can thus be directly compared to the Smithian ones of Brühwiler et al. (2010b, updated according to Brühwiler et al., 2012a and the new classification established in Ware et al., submitted-a), thus significantly expanding downward the available high-resolution time window within the Early Triassic of the NIM.

2.1. Taxonomic data sets

In the Salt Range, Dienerian ammonoids were collected from four areas (Nammal, Chiddru, Amb and Wargal). Several sections were sampled in these four areas, and a composite section was constructed for each of them based on bed-by-bed correlations, an approach recommended by Guex (1991) for enhancing the completeness of the stratigraphic ranges of species. In Spiti, Dienerian ammonoids were collected from eight sections distributed in three areas (Mud, Guling and Lalung). Details concerning the localities, the stratigraphy and ammonoid taxonomy are given in Ware et al. (submitted-a) for the Salt Range and in Ware et al. (submitted-b) for Spiti.

The first step consists in a detailed revision and standardization of the ammonoid taxonomy, with special emphasis on intraspecific and ontogenetic variation. The results of this revision are presented in Ware et al. (submitted-a and b). This led to an improved understanding of the taxonomy of Dienerian ammonoids, inclusive of above the specific level, where many genera were so far poorly defined. A grand total of 47 species were recognised. For the biochronological analysis, occurrences based on poorly preserved material or based on rare taxa found in only a single sample were

removed from the initial dataset. For the Dienerian, five such species with unique occurrences were omitted and then re-inserted in the dataset after completion of the biozonation.

2.2. Unitary Association method

The biozonation presented here is based on the Unitary Associations (UA) method of Guex (1991). A general account of the advantages of this method is given in Brühwiler et al. (2010b), and for the exhaustive description of the UA method the reader is referred to Guex (1991), Monnet and Bucher (2002) and Monnet et al. (2015). The UA analysis was performed with the palaeontological data analysis software PAST (Hammer et al., 2001). This method has several crucial advantages. First, UAs are discrete (non-continuous) time bins consisting of unique and mutually exclusive assemblages of taxa, isolated from each other by intervals of separation, thus faithfully reflecting the discontinuous nature of the fossil record. These exclusive assemblages are maximal sets of co-occurring species and can accommodate any later modification of the data set without creating conflicting superpositional relationships such as is the case for all approaches based on the fluctuating positions of First Occurrences and Last Occurrences. Second, Escarguel and Bucher (2004) demonstrated that such zones based on the maximal association principle provide reliable counts of species richness, whatever the unknown duration of each UA-zone.

The construction of UA-zones includes the following steps. First, an occurrence matrix for every section of the Salt Range and Spiti is built (Appendix A – Table 1). Then, the regional UAs for the Salt Range and Spiti are computed separately using PAST. The regional zonations and species occurrences obtained (Appendix A – Table 2) are thus treated as a two sections dataset, which is again processed with PAST to obtain UAs at the NIM palaeogeographical level. Taxa with a single occurrence that were initially removed from the dataset are then dated and re-inserted into the zonation. Finally, UAs having a poor lateral reproducibility and/or which are based on very rare

characteristic species are merged to construct the UA-zones sequence for the NIM (see discussion in Section 4.1).

2.3. Diversity dynamics

Analyses of diversity dynamics follow the same procedure as Brühwiler et al. (2010b). Species richness corresponds to the number of species in a UA-zone, and originations and extinctions correspond to the number of species that appear and disappear between two successive zones. Origination rate is the number of originations divided by the species richness of the subsequent zone; extinction rate is the number of extinctions divided by the species richness of the previous zone. The turnover is the sum of originations and extinctions, and the turnover rate is the turnover divided by the total species richness of the two corresponding successive zones. A rarefaction analysis on the species richness was conducted using PAST to estimate the bias induced by sample size on species counts. This potential sampling bias was further investigated with incidence-based total richness estimators calculated with Estimates (Colwell, 2009). An additional analysis at the genus level was performed, including the generic richness and the corresponding originations, extinctions and turnovers. These results were completed with a poly-cohort analysis (Raup, 1978, 1986; Foote, 1988; Hartenberger, 1988; Brayard et al., 2009). Finally, the respective contribution of each family to species richness (both in absolute and relative values) was computed.

2.4. Palaeoenvironmental proxies

The results of the biodiversity analysis are compared to various palaeoenvironmental proxies obtained from the same sections in the Salt Range. These include palynofacies data from the Nammal section in the Salt Range, carbonate and organic carbon isotopes from Nammal, Chiddru and Amb in the Salt Range (Hermann et al., 2011; Schneebeli-Hermann et al., 2012), and oxygen isotopic

composition of conodonts from Nammal (Romano et al., 2013). Since these palaeoenvironmental proxies are obtained from the same sections from which ammonoid data are derived, it is possible to calibrate them with our new biostratigraphic scheme by using the following piecewise approach. When a data point comes from a bed directly assigned to a UA-zone or is bracketed by beds belonging to the same UA-zone, this point is plotted in the middle of the UA-zone. When several data points are available within one UA-zone, they are plotted at equidistance, in stratigraphic order, within this UA-zone. When one or several data points come from an interval bracketed by two successive UA-zones, they were plotted at equidistance between these two UA-zones. Finally, when one or several data points are bracketed by beds containing faunas characteristic of two non-consecutive UA-zones (i.e. when one or several UA-zones are missing in the section where the data comes from), they were placed at equidistance between the two corresponding UA-zones.

3. Results

3.1. Biochronology

In the Salt Range, the procedure described above led to the recognition of 13 UAs within the Dienerian. However, two of these UAs (SR9 and SR10, see Appendix A – Table 2) are lumped together, because they are only differentiated by a very rare species (*Mullericeras spitiense*). Therefore, 12 UA-zones are recognized for the Dienerian of the Salt Range (fig. 2). These precisely correspond to the 12 empirical Dienerian ammonoid faunas previously established by Ware et al. (submitted-a). For the Spiti region, 11 Dienerian UAs were detected. Again, two of them (SP2 and SP3, see Appendix A – Table 2) were lumped together, as the oldest UA differs from the subsequent one only by the presence of two very rare species (*Ussuridiscus ornatus* and *U. ventriosus*). The resulting 10 UA-zones also correspond to the empirical succession of 10 faunas recognized by Ware et al. (submitted-b). These 10 UA-zones in Spiti are identical to 10 out of the 12 UA-zones of the Salt

Range, within the limits of a few endemic species only. Hence, 12 UA-zones are defined at the pooled level of the NIM. The resulting synthetic range chart shows the occurrences of the different species in these 12 UA-zones of the NIM (Fig. 3). Two of these (DI-7 and DI-12) occur only in one area (Nammal) of the Salt Range. Usually, such poorly laterally reproducible UA-zones are merged with one of the adjacent UA-zones. However, this option was not chosen here as in both cases, the only taxa in common with the adjacent UA-zones are long ranging taxa. Thus, there was no objective way of deciding with which of the two neighbouring UA-zones these should be merged with. Until additional data become available, these two UA-zones only found in Nammal are kept as valid.

Additionally, a new threefold subdivision of the Dienerian into early, middle and late Dienerian is proposed. The early Dienerian is characterized by the co-occurrence of *Gyronites* and *Ussuridiscus* together with the youngest representative of ophiceratids (*Ghazalaites*). It includes the first three UA-zones (DI-1to DI-3). The middle Dienerian is characterized by the co-occurrence of *Ambites* and *Mullericeras*, and comprises five UA-zones (DI-4 to DI-8). The late Dienerian includes the oldest paranoritids (e.g. *Vavilovites*, *Koninckites*, *Awanites*) and hedenstroemiids (*Clypites* and *Pseudosageceras*) and is composed of four UA-zones (DI-9 to DI-12).

The early Smithian biozonation and synthetic range charts have been established by Brühwiler et al. (2010b, 2012a).These data are included in the present study and are used in the subsequent analyses.

3.2. Biodiversity dynamics

For the Dienerian, species richness (fig. 4) shows the same trends in both basins, which leads to a robust pattern at the pooled level of the NIM. A total of 43 species in the Salt Range and 37 species in Spiti were identified, representing 47 species for the Dienerian of the NIM. Species richness is generally rather low in the Dienerian, fluctuating between 3 and 8 species per UA-zone in the Salt Range, between 2 and 9 in Spiti, and between 3 and 9 for the NIM. It reaches a distinctive

first peak in the early Dienerian (DI-2) with 8 species in the Salt Range and 9 in Spiti and for the NIM. In the middle Dienerian, species richness is stagnating at low values, with usually only 4 species per UA-zone, with minor fluctuations (up to 6 in the latest middle Dienerian [DI-8] of the Salt Range). The lowest diversity is recorded in DI-7 with only 3 species. This UA-zone is actually only known from Nammal in the Salt Range, which could lead to underestimate its diversity value. In the late Dienerian, a few minor differences can be seen between the Salt Range and Spiti. In the Salt Range, species richness increases from 4 to 7 species from DI-9 to DI-11. The low diversity in DI-12 is probably influenced by the fact that it has a unique occurrence (Nammal). In Spiti, only 2 species were found in DI-9, and the species richness then increases to reach 5 species in DI-11. The DI-9 zone is very well documented in Spiti, suggesting that this very low diversity is a genuine signal. The 2 additional species found to have their first occurrence in DI-9 in the Salt Range have their first occurrence later in DI-10 in Spiti, thus illustrating the diachronism of first occurrences between different basins. For the early Smithian, significant discrepancies are observed between the Salt Range and Spiti (Fig. 4). In the Salt Range, species richness peaks in SM-3 with 8 species, and then drops back to values similar to the late Dienerian, whereas in Spiti it stays low from SM-1 to SM-4 and peaks in SM-5 with 10 species. At the scale of the NIM, the following general trends can be recognised: (1) a first minor diversity peak in the early Dienerian; (2) a very low diversity in the middle Dienerian; (3) a very slight increase in the late Dienerian; (4) a rather high and stable diversity in the earliest early Smithian (SM-1 to SM-4); (5) a sharp increase in diversity in the late early Smithian.

The rarefied diversity curves (fig. 5) closely match the species richness curves, indicating that there are no important sampling effort and/or preservation biases in our data. The only difference concerns the early Smithian at the pooled level of the NIM. Only a gradual increase in diversity is recorded there instead of a two-phased recovery as shown by the raw diversity data (with first a plateau followed by a sharp increase in diversity). The Chao2 and Jackknife2 indices (Appendix A-Table 3) are nearly identical to the species richness, giving further indication of absence of bias in our

sampled data. However, the Chao2 confidence intervals and Jackknife2 bootstrapped standard error are much more important in the early Smithian than in the Dienerian, indicating greater dissimilarities between the Salt Range and Spiti during the early Smithian than during the Dienerian. It should be noted that these two indices were calculated only for two basins, so data of similar age from other basins would be necessary to further test how these trends are laterally reproducible.

Originations and extinction rates (fig. 6) are very high during the entire studied interval, generally above 50% and occasionally reaching 100%. Extinctions exceed originations at the early-middle and middle-late Dienerian transitions. In the early Dienerian, both extinctions and originations are very high. Originations exceed extinctions between DI-1 and DI-2, while it is the opposite between DI-2 and DI-3. In the middle Dienerian, extinctions and originations are relatively well balanced and low, except around DI-7, a zone which could be affected by a sampling bias. In the late Dienerian, originations tend to slightly exceed extinctions, but both are rather low. The changes around DI-12 should not be taken into account as this zone is comparatively poorly documented. In the early Smithian, originations generally exceed extinctions, with higher absolute values.

Turnover rates (fig. 7) are always very high, above 60% and sometimes reaching 100%. The highest percentages are recorded at the early-middle and middle-late Dienerian transitions, and within the early Smithian. The lowest values occur within the middle and the late Dienerian.

Figure 8 shows the generic richness and the extinction, origination and turnover counts and rates at the generic level for the NIM. The generic richness follows the general trends recorded at the species level, except that the curve appears slightly smoothed out. The generic richness is moderately high in the early Dienerian (4 to 5 genera), stagnates at low levels throughout the middle Dienerian with only 3 genera, and then starts increasing progressively in the late Dienerian before peaking in the late early Smithian with 9 genera. Origination, extinction and turnover rates at the genus level also follow the general trends observed at the species level, but with lower values. They reach their highest values at the early-middle and middle-late Dienerian boundaries. They are very low in the early and late Dienerian, where originations usually exceed extinctions. In the middle

Dienerian, they all drop down to zero, meaning that the same 3 genera occur throughout this interval and that the species richness fluctuations in this time interval are only the results of speciation events within these three lineages. In the early Smithian, their values become rather high (except between SM-3 and SM-4), and originations usually exceed extinctions.

Brayard et al.'s (2009) contour graphs of the ammonoid poly-cohort matrix (PCM; fig. 9A) highlights the high evolutionary rate of ammonoids during the Early Triassic compared with previous and subsequent times, as shown by the extreme contraction of survivorship and prenascence contour lines. A similar analysis was performed on our regional dataset at the species level (fig. 9B), allowing us to zoom into the Dienerian and early Smithian part of the Early Triassic. Here too, the survivorship and prenascence contour lines are extremely contracted and mirror each other, thus reflecting the very high turnover rates throughout the Dienerian (most species are confined to one single zone). The contour lines even fall to zero at the early-middle and middle-late Dienerian boundaries, meaning a complete replacement of the faunas between the three main subdivisions of the Dienerian. The three-fold subdivision of the Dienerian appears here again to be strongly supported. Moreover, it also reflects the four diversity phases previously discussed, with a first weak recovery in the early Dienerian, an extinction phase at the early-middle Dienerian boundary followed by a time interval of persistent low diversity, a renewal of the faunas at the middle-late Dienerian boundary followed by a slight diversification, followed by the early Smithian re-diversification, i.e. the accumulation of longer ranging new species.

The graph showing the respective contributions of the different families in terms of species richness (fig. 10) gives some more insights about the diversity dynamics. The number of families stays rather low during the entire interval, with a maximum of seven families (plus two genera placed in incertae sedis) in the latest early Smithian. The early and middle Dienerian are dominated by Gyronitidae, which co-exist with Proptychitidae and Mullericeratidae. The early Dienerian differs from the middle Dienerian by the inclusion of the last representatives of Ophiceratidae, whereas the middle Dienerian contains only the three other previously mentioned families. In the late Dienerian,

Gyronitidae are replaced by Paranoritidae (which also dominate the faunas), while Mullericeratidae are replaced by Hedenstroemiidae. Proptychitidae disappear at the middle-late Dienerian boundary (unless the genus *Kingites,* here placed in Incertae Sedis, is included in proptychitids; see Ware et al., submitted-a for details concerning the classification). In the early Smithian, several new families successively appear: Flemingitidae, Kashmiritidae, Aspenitidae and Dieneroceratidae. The faunas are alternatively dominated by Paranoritidae and Flemingitidae. Interestingly, Proptychitidae regionally intermittently reappear in the early Smithian.

4. Discussion

4.1. Biochronology

No conflicting stratigraphic relationships between taxa were found in our dataset, highlighting the excellent quality of our taxonomic and biostratigraphic primary data. As a consequence, the zonation established here confirms the empirical scheme previously established by Ware et al. (submitted-a, b). This new Dienerian biochronological scheme, with 12 UA-zones grouped into three subdivisions, strongly contrasts with all previously established Dienerian biozonation. For example, Tozer (1965, 1994), when erecting the Dienerian stage and proposing what is thus far the most widely used ammonoid biostratigratigraphic scheme, recognised only four sub-zones, grouped into two zones. The main reason for this difference is the scarcity of carbonate in the Dienerian of Arctic Canada, which impairs the quality of the ammonoid record in the high latitudes (see Monnet and Bucher, 2005 for the well documented example of the Anisian across North America). Moreover, the correlations established by Tozer (1994) between Arctic Canada and British Columbia are problematic. The specimens he identified as *Proptychites candidus* in British Columbia are here assigned to *Proptychites lawrencianus* (see Ware et al., submitted-a for taxonomy). Hence, the Candidus zone cannot be recognised in British Columbia. In British Columbia, *Proptychites*

lawrencianus is also associated with specimens here synonymised with *Ambites lilangensis*, thus indicating that this fauna can directly be correlated with our UA-zone DI-8. As the Arctic Candidus Zone and UA-zone DI-8 do not share any characteristic species, they do not correlate. Additional observations by one of the authors (D.W.) on unpublished material of Tozer's collection from British Columbia indicate the presence of at least three other of our UA-zones in this region: DI-5, DI-6 and DI-10. These faunas generally come from scattered occurrences in British Columbia, often without superpositional information. This nevertheless indicates that the Dienerian faunas of British Columbia have at least some affinities with those of the NIM, whereas those of Arctic Canada are presently too poorly known for any meaningful comparison. Additional investigations in British Columbia should lead to a more complete biozonation and a better understanding of the affinities of these faunas with the NIM and Arctic Canada. The correlations of the biostratigraphic scheme established here with those of Canada and other regions are detailed in Ware et al. (submitted-a).

The duration of each UA-zone can be estimated using the latest high-precision single zircon U-Pb ages obtained from South China. An age of 251.88 ± 0.031 Ma for the Permian-Triassic boundary has been recently proposed by Burgess et al. (2014). An age of 251.22 ± 0.2 Ma for the early Smithian *Kashmirites kapila* beds (corresponding here to SM-5 according to Brühwiler et al., 2010b) is provided by Galfetti et al. (2007b). A duration of ca. 0.66 ± 0.231 My can thus be inferred for the time interval comprised between the Permian-Triassic boundary and SM-5. Krystyn et al. (2004) showed that the Griesbachian of Spiti can be subdivided into three ammonoid zones. Therefore, 19 zones have been identified in the NIM between the Permian-Triassic boundary and SM-5, which yields an average maximal duration of 34.7 ky per zone (including the intervals of separation between the UA-zones). This average duration is shorter than that obtained by Brühwiler et al. (2010b) for the Smithian of the NIM, but taking the error embedded in the age of the *Kashmirites kapila* beds into account, it is better considered to be of the same order of magnitude.

4.2. Diversity dynamics

The four following main phases in diversity patterns can be identified for Dienerian and early Smithian ammonoids from the NIM: (1) a first small peak of recovery in the early Dienerian; (2) an extinction followed by a very low diversity throughout the middle Dienerian; (3) a slow increase in diversity in the late Dienerian; (4) a much more rapid increase in diversity associated with the appearance of several new families in the early Smithian. These changes in diversity are associated with very high turnover rates, especially at the early-middle and middle-late Dienerian boundaries where entire faunas are replaced. Although the early Smithian shows comparably high turnover rates, it differs from the Dienerian in having some longer lived species.

Three hypotheses can explain the temporary absence of Proptychitidae during the late Dienerian: (1) an apparent absence due to sampling effort; (2) a convergence problem between phylogenetically distant species of different age (e.g. globose and constricted forms such as *Juvenites* of middle Smithian age and *Arnautoceltites* of late Spathian age); (3) the local disappearance of this family in the NIM, followed by re-colonisation of this region from the global pool. As Proptychitidae are usually not very abundant, particularly in the early Smithian, the first hypothesis may well apply for SM-3 and 4. It can however definitely be rejected for the late Dienerian as DI-10 and DI-11 yielded the most abundant material, representing more than a third (1504 out of a total of 4151 specimens) of all the ammonoids collected in this study. The second hypothesis is also unlikely, as Proptychitidae constitute a well-defined family, easily differentiated from other co-occurring families by the presence of indentations on the lobe sides (see Ware et al., submitted-a for detailed descriptions). As a consequence, the absence of Proptychitidae in the late Dienerian of the NIM suggests a local and temporary ecological exclusion. Since the genus *Vavilovites* is here assigned to Paranoritidae (and not Proptychitidae as in Tozer, 1994), no proptychitids from unequivocal late Dienerian strata are known so far.

Several palaeoenvironmental proxies (fig. 11) from the studied NIM sections provide some insights on possible causes of these diversity changes. Palynofacies analysis (Hermann et al., 2011)

indicates three phases: (1) a strong terrestrial influence in the early Dienerian (demonstrated by the high relative abundance of opaque phytoclasts) indicating a low sea level; (2) dysoxic to anoxic conditions and higher sea level (indicated by high relative abundance of amorphous organic matter [AOM]) in the middle and late Dienerian and in the earliest Smithian; (3) a return to normal oxic conditions and high sea level (suggested by high relative abundance of acritarchs and only minor contribution of AOM), for the rest of the early Smithian.

Oxygen isotopes measured from biogenic phosphate (Romano et al., 2013; Fig. 11b) and organic carbon isotopes (Hermann et al., 2011; Fig. 11d) tend to track each other and also reveal three phases: (1) moderately heavy values in the early Dienerian; (2) very light values in the middle and late Dienerian, with lightest values in the middle Dienerian; (3) heavy values in the early Smithian. The carbonate carbon isotope record from Nammal (after Hermann et al., 2011) shows rather constant values during most of the Dienerian. However, these data record a 3 ‰ positive excursion at the Dienerian-Smithian boundary.

The comparison of our diversity results with these palaeoenvironmental proxies suggests that early Dienerian and early Smithian ammonoids regional recovery is concomitant with relatively oxygenated and cold water conditions. The middle Dienerian diversity low is concomitant with a probably anoxic sediment-water interface and warmer sea water temperatures. Coupling with relative sea level changes in the Salt Range is not obvious as the entire Dienerian has been interpreted as a main transgressive phase and the early Smithian as a regressive phase (Hermann et al., 2011). Noteworthy, the middle Dienerian diversity minimum occurs during the transgression, thus largely pre-dating the high-sea level stand that coincides with the Dienerian-Smithian boundary. In Spiti, Early Triassic rocks are largely over-mature thus preventing environmental inferences from palynofacies and oxygen isotopes. However, the same trends in facies oxygenation and relative sea-level changes also emerge from sedimentological and taphonomical criteria in Spiti. There, rocks of middle and late Dienerian age consist of black shales containing early diagenetic, organic-rich limestone concretions yielding complete fishes (Ware et al., submitted-b), thus contrasting with the

grey and bioturbated ledge-forming nodular limestone of early Smithian age (i.e. "*Flemingites* beds", Galfetti et al., 2007a).

When brought into a larger palaeogeographical perspective, it appears that anoxic events during the Early Triassic are concentrated in two main episodes coinciding with the lowest relative diversity and reduced morphological disparity of ammonoids: a middle to late Dienerian event and a late Smithian event (Galfetti et al., 2007c; Brosse et al., 2013; Bucher et al., 2013). Evidence for the middle to late Dienerian anoxic episode on outer shelves is found in the following well-dated, ammonoid-bearing areas: Nevada (Ware et al., 2011), South China (Galfetti et al., 2008) and southern Tibet (Brühwiler et al., 2009). Dark shales of similar age are also recorded in Primorye (Shigeta et al., 2009) and anoxic shales of Dienerian age are described from British Columbia (Orchard and Zonneveld, 2009) and Arctic Canada (Grasby et al., 2013). The present diversity results also highlight that at least at the scale of the NIM, the highly dynamical recovery pattern with ups and downs, support previous hypotheses of a rapid global ammonoid rediversification briefly interrupted by several extinctions events (e.g. middle Dienerian, end Smithian; see Brayard et al., 2006, 2009). Similarly detailed studies and additional sampling effort in other provinces would be necessary to enhance the quality of global correlations in order to test whether the diversity dynamics established here really constitute a global signal.

5. Conclusions

The synthesis of the two recent works focusing on the taxonomical revision and detailed biostratigraphy of Dienerian ammonoids from the Salt Range (Ware et al., submitted-a) and from Spiti (Ware et al., submitted-b) allowed us to construct a new biostratigraphic scheme of unprecedented high resolution based on the Unitary Associations method. A total of 12 zones can be recognized for the Dienerian. On the basis of the turnover at the genus level, these zones are grouped into early, middle and late Dienerian. The U-Pb ages obtained in South China (Galfetti et al.,

2007b, Burgess et al., 2014) allow the calculation of an average maximal duration of 34.7 ky per ammonoid zone (inclusive of the separation intervals).

Based on this new zonation, ammonoid biodiversity dynamics for the Dienerian and early Smithian of the NIM show the following four phases: (1) a moderately high diversity in the early Dienerian; (2) a decline followed by a very low diversity throughout the middle Dienerian; (3) a very slight increase in diversity in the late Dienerian; (4) an important radiation in the early Smithian. Very high turnover rates are observed throughout the Dienerian, thus confirming the results obtained at a global scale and with a less well resolved time scale by Brayard et al. (2009). The very low diversity in the middle and late Dienerian is associated with warm temperatures and an anoxic episode on continental shelves in the low palaeolatitudes. This sequence of events is at variance with the simplistic model of a protracted and progressive recovery following the end-Permian mass extinction (e.g. Chen & Benton, 2012, see further critique of this model in Scheyer at al., 2014). It leads to propose a more realistic model consisting of alternating diversification and extinction phases related to unstable environmental conditions. An interesting and open forthcoming step is how the high-resolution ammonoid diversity dynamics of the Griesbachian compares to those of the Dienerian and the Smithian.

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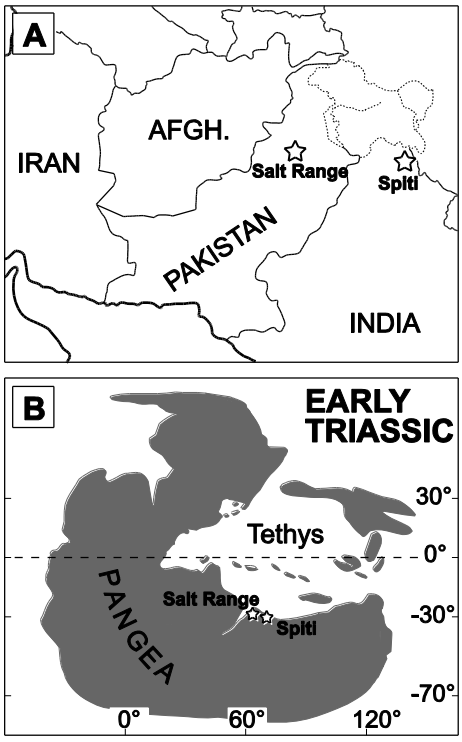

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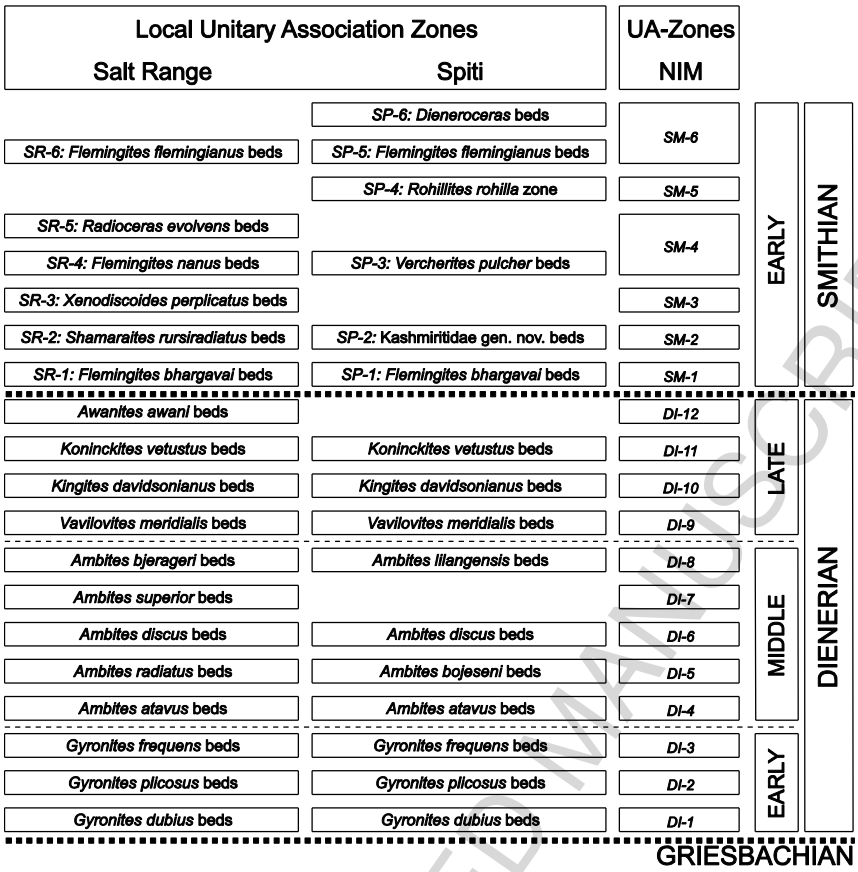

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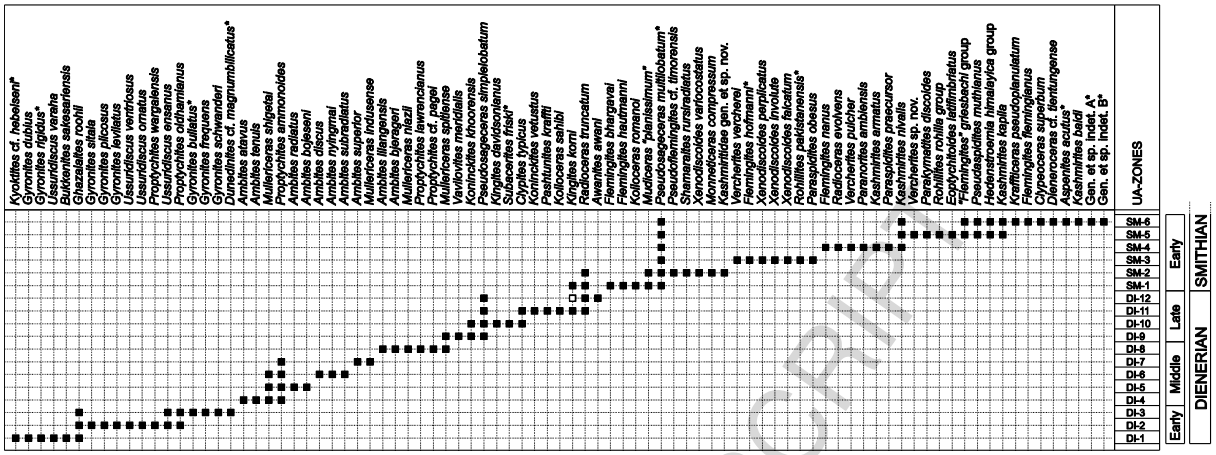

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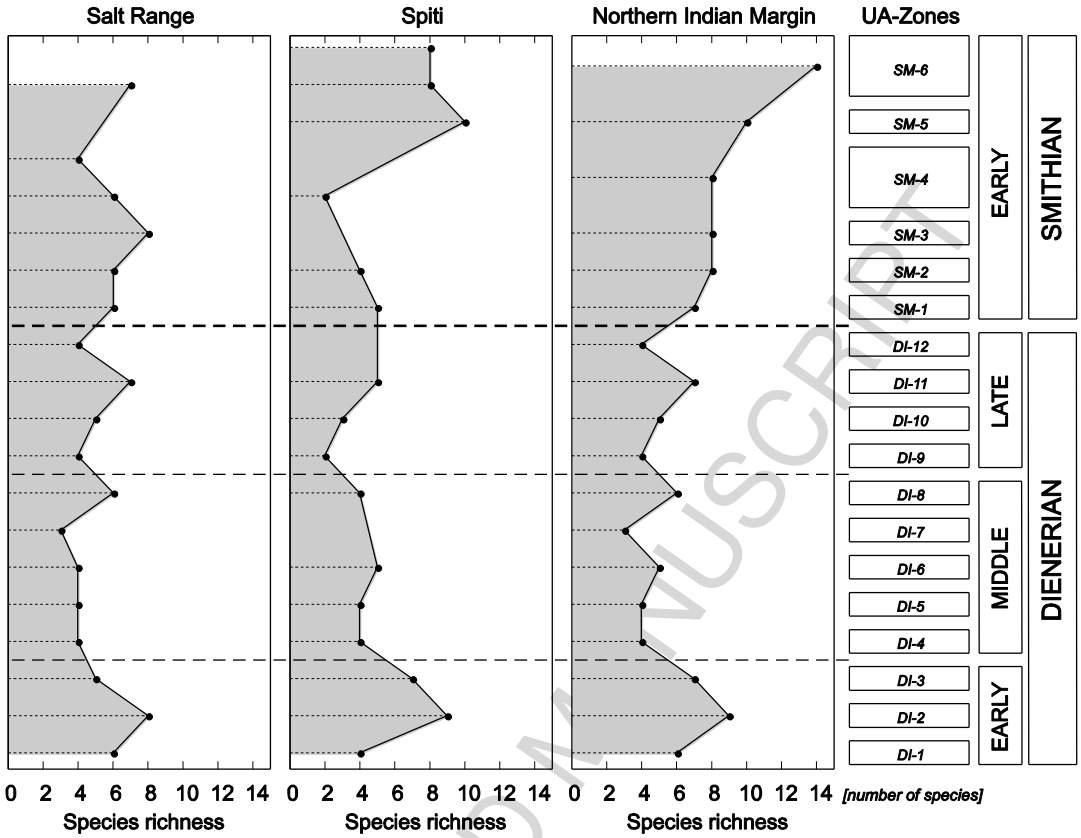

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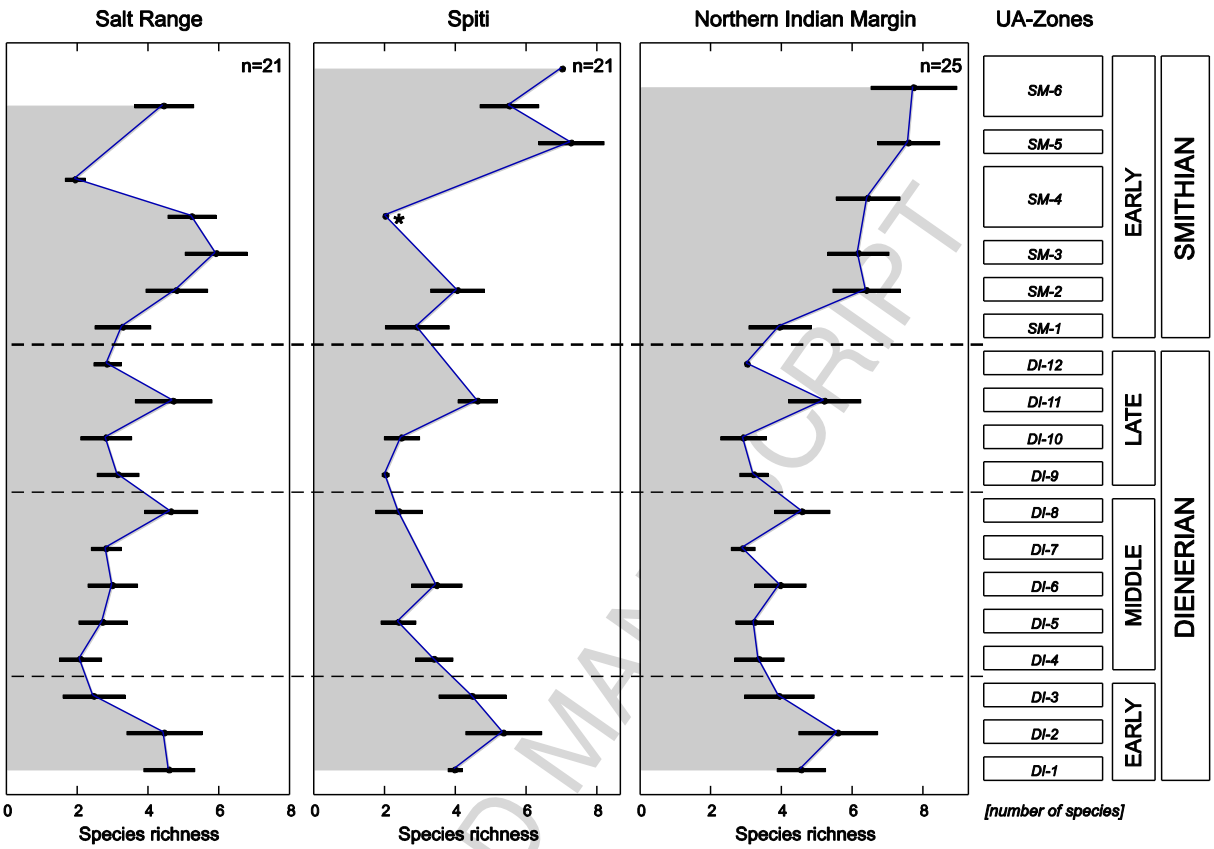

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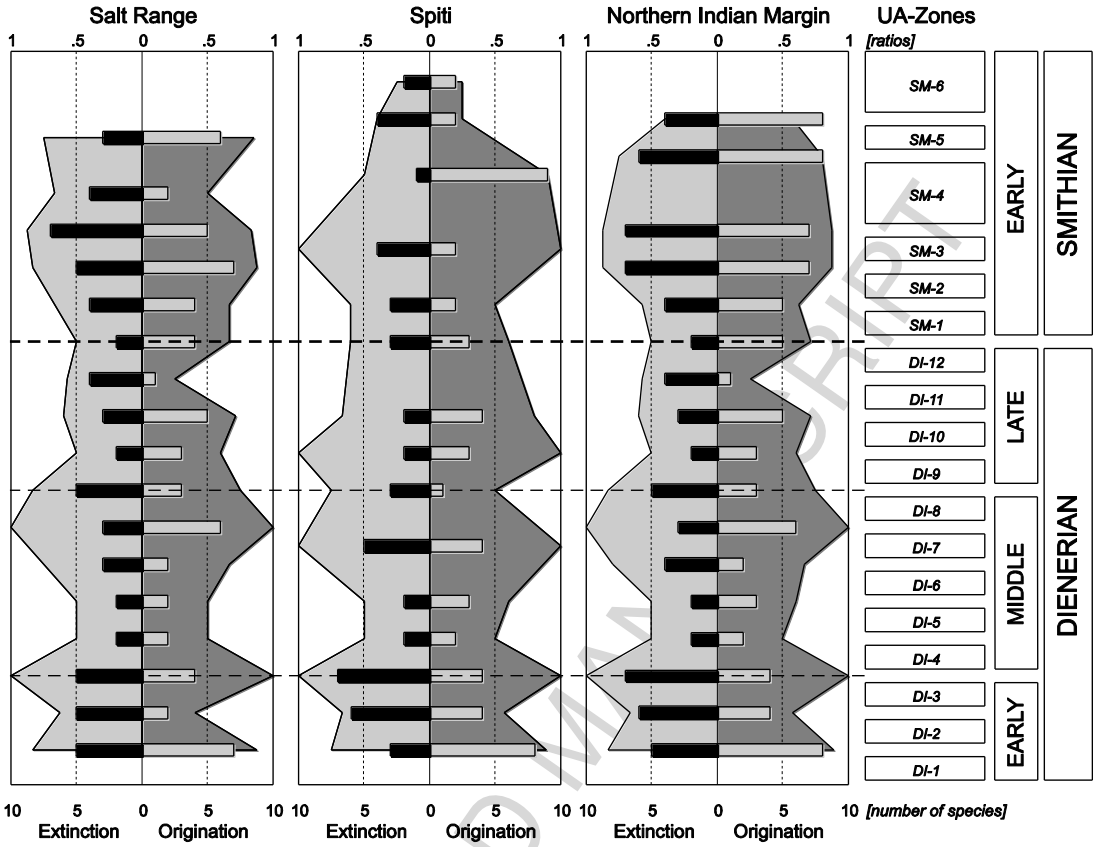

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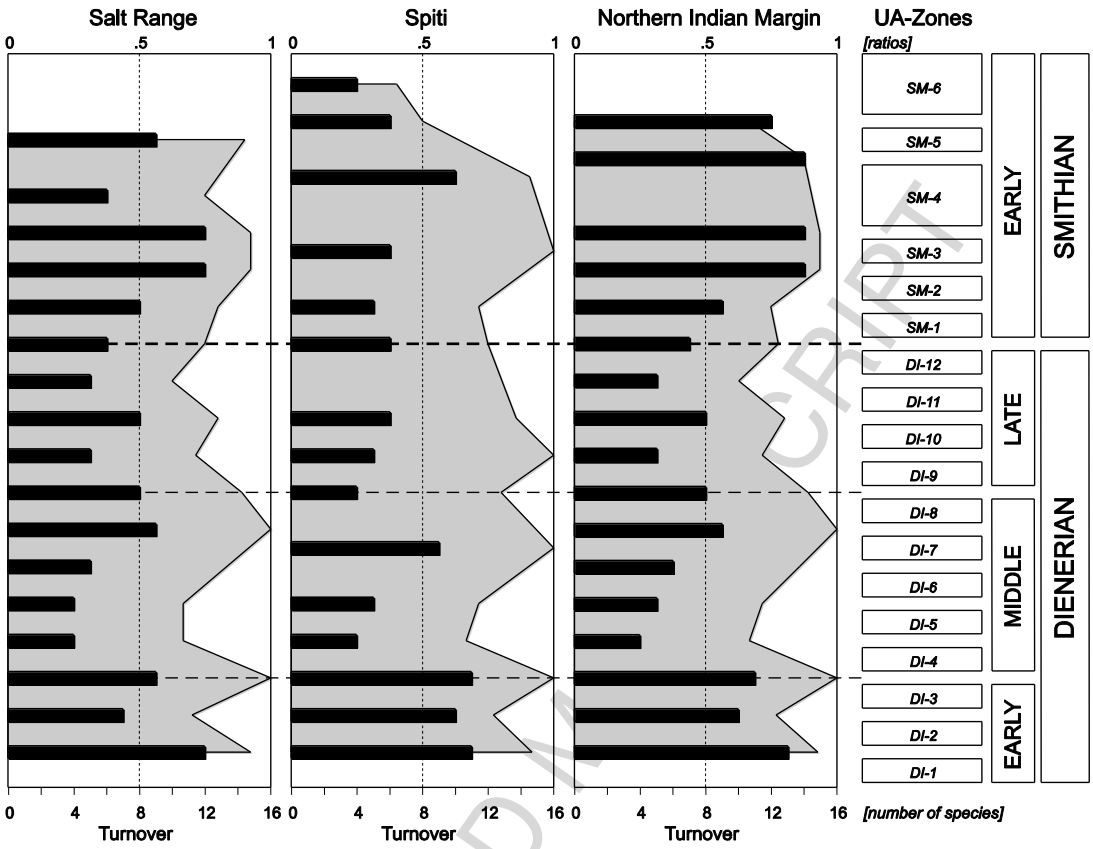

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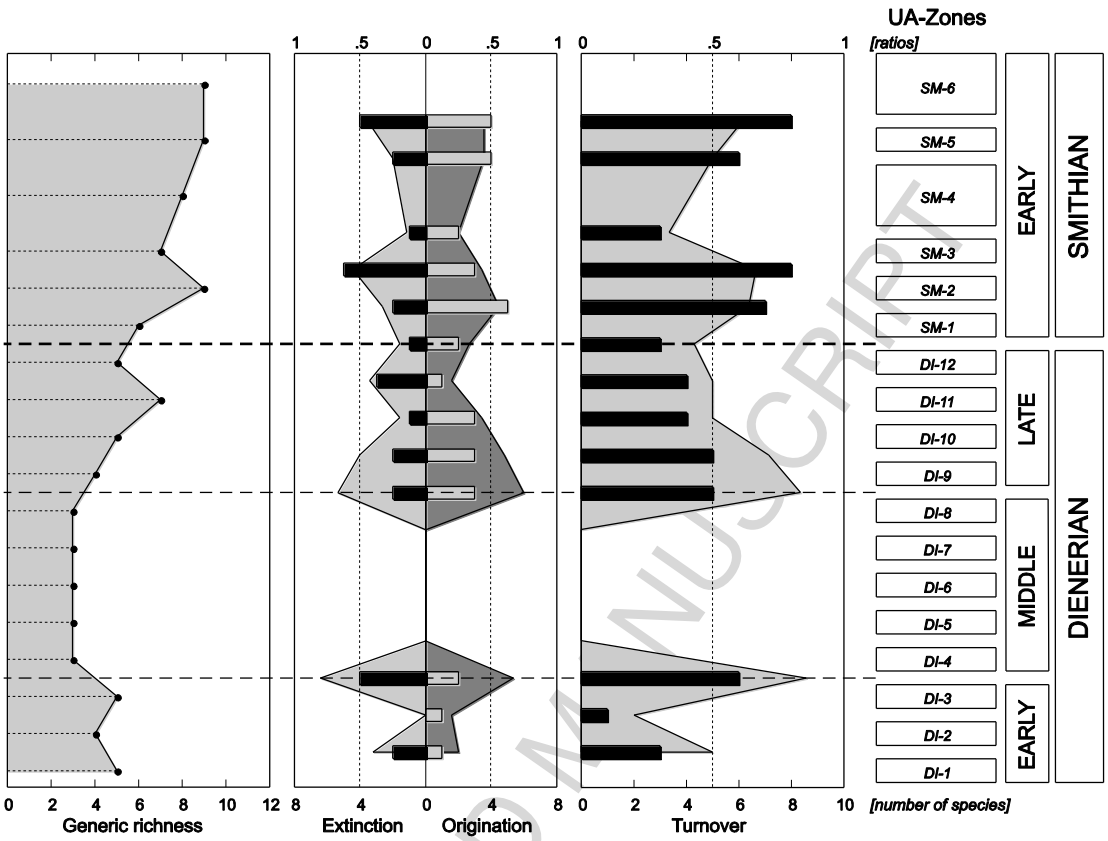

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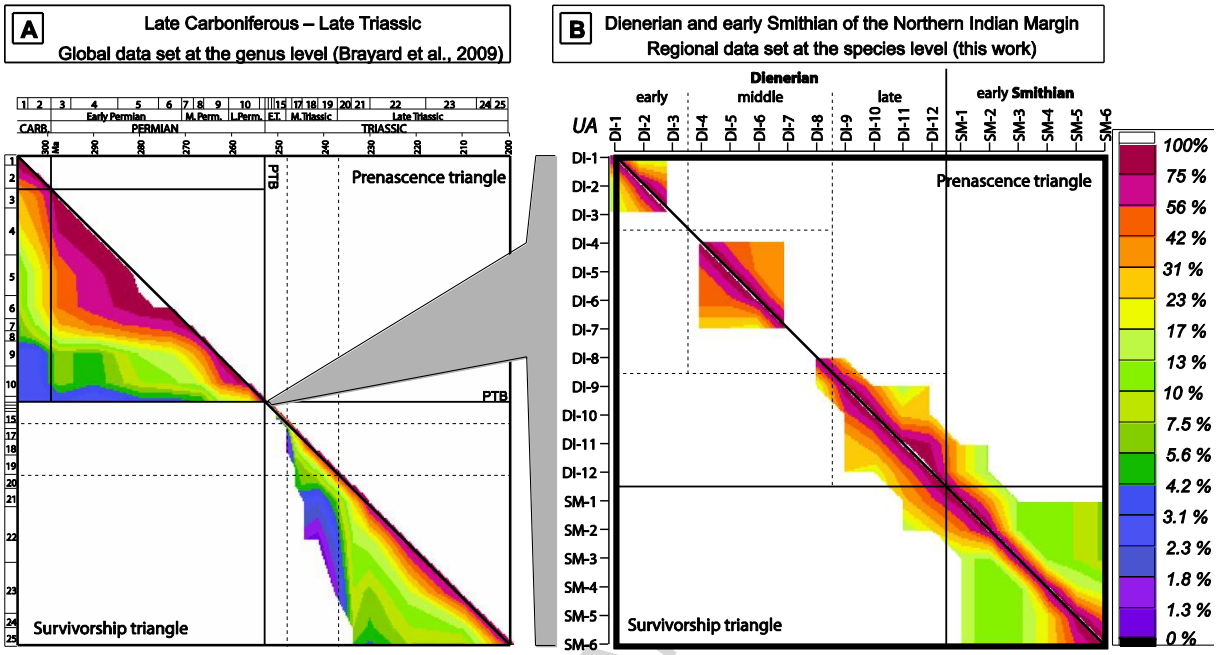

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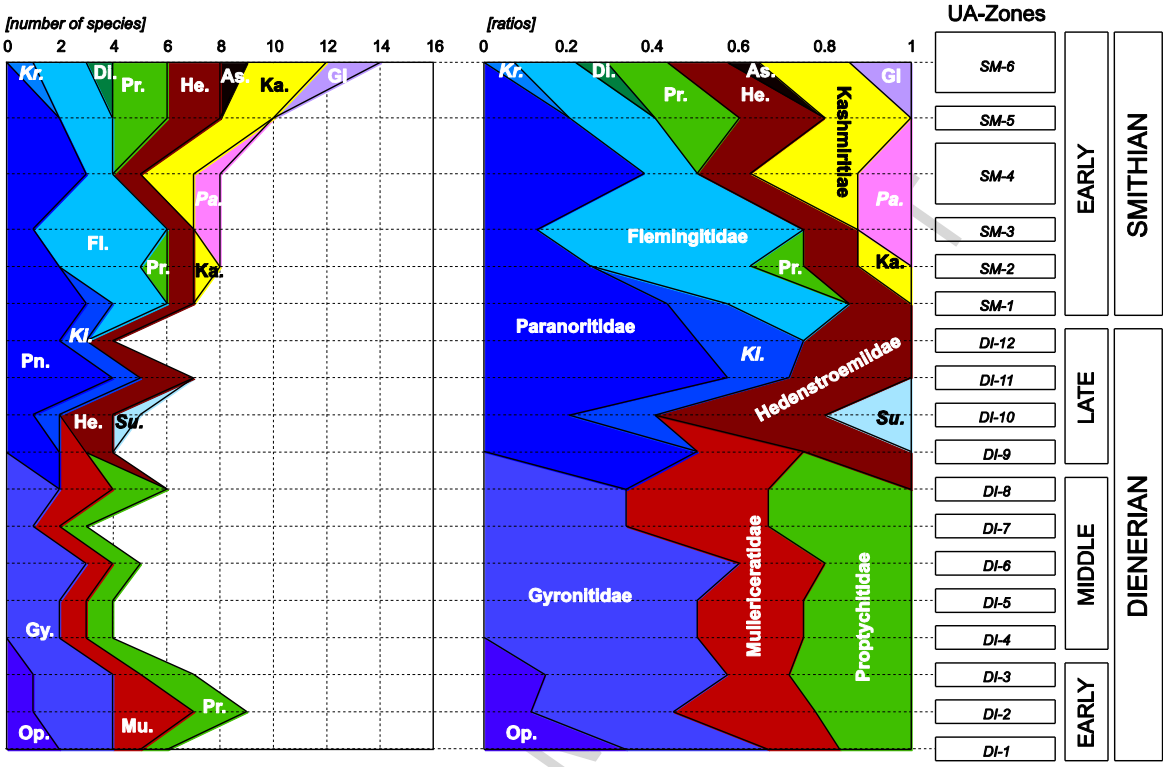

Figure 10

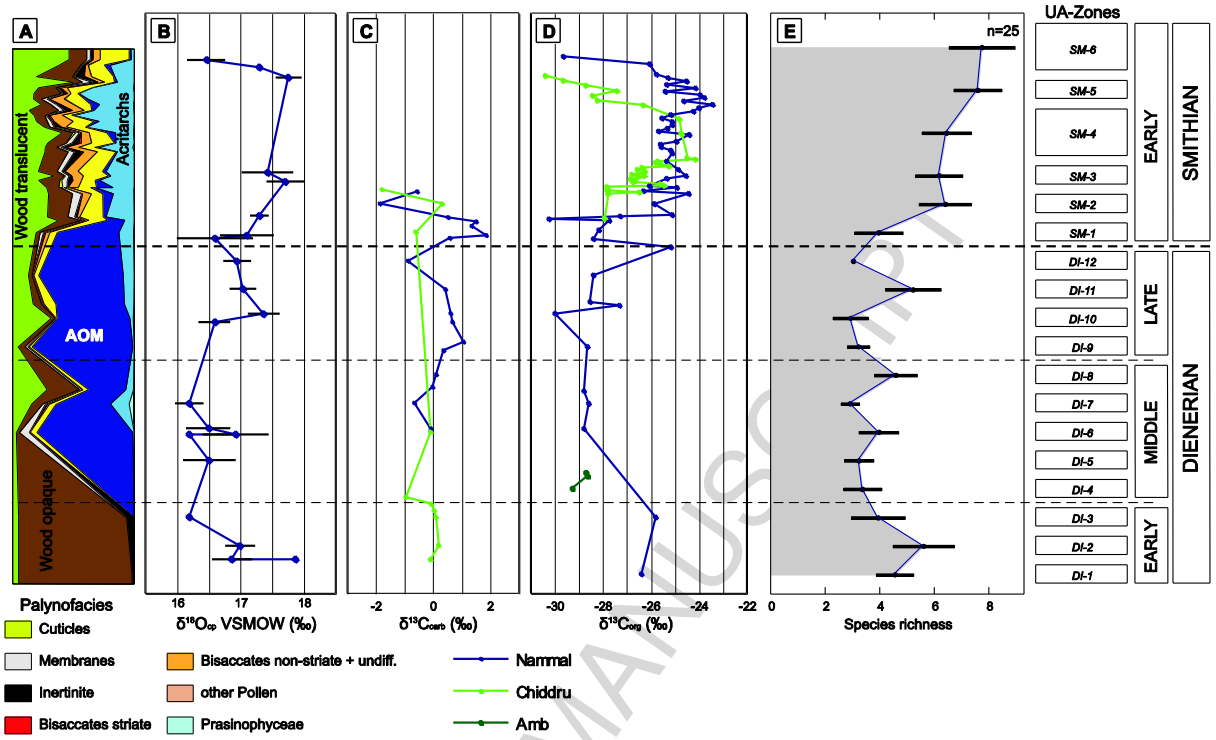

Figure 11

Figure captions

Fig. 1. [A] Situation of the Salt Range and Spiti; [B] simplified early Triassic palaeogeography (modified after Brayard et al., 2006) with the position of the Salt Range and Spiti.

Fig. 2. Unitary Associations (UAs) of each basin and inter-basin UA-zonation.

Fig. 3. Synthetic range chart with the distribution of Dienerian and early Smithian ammonoid species for the Northern Indian Margin. White squares indicate virtual occurrences. Species marked by an asterisk (*) were omitted in the dataset for the construction of the UAs (see text). They are dated and reincorporated into the range chart at the end of the processing.

Fig. 4. Plots of ammonoid species richness for the Salt Range, Spiti and the Northern Indian Margin.

Fig. 5. Rarefied species richness curves and associated 95% confidence intervals. The curves for the Salt Range and Spiti have been rarefied to a sample size of *n* = 21; that of the Northern Indian Margin to a sample size of *n* = 25. The asterisk (*) marks a sample of very small size (6 specimens) that has not been included in the rarefaction analysis. Virtually present species (Fig. 4) are not included within this dataset.

Fig. 6. Values (bars) and percentages (shaded areas) of ammonoid species origination and extinction throughout the Dienerian and early Smithian.

Fig. 7. Values (bars) and percentages (shaded areas) of turnover of ammonoid species throughout the Dienerian and early Smithian.

Fig. 8. Generic richness, origination, extinction and turnover throughout the Dienerian and early Smithian of the Northern Indian Margin.

Fig. 9. [A] Brayard et al.'s (2009, modified) contour graphs of the ammonoid poly-cohort matrix (PCM) for a global dataset at the genus level spanning the Late Carboniferous-Late Triassic time interval. Each column of the PCM records the prenascence (upper triangle) and survivorship (lower triangle) percentages of a target assemblage located on the diagonal "100% cell". Abbreviations: PTB, Permian-Triassic Boundary; 1, Kasimovian; 2, Gzhelian; 3, Asselian; 4, Sakmarian; 5, Artinskian; 6, Kungurian; 7, Roadian; 8, Wordian; 9, Capitanian; 10, Wuchiapingian; unlabelled successive intervals, Changhsingian, Griesbachian, Dienerian, Smithian; 15, Spathian; 16, Early Anisian; 17, Middle Anisian; 18, Late Anisian; 19, Ladinian; 20, Early Carnian; 21, Late Carnian; 22, Early Norian; 24, Late Norian; 25, Rhaetian. [B] Contour graph of the ammonoid PCM for the regional dataset at the species level for the Dienerian and early Smithian of the Northern Indian Margin.

Fig. 10. Absolute and relative species richness for each Dienerian and early Smithian ammonoid family plotted against the UA-zonation of the Northern Indian Margin. Abbreviations for the families: As, Aspenitidae; Di, Dieneroceratidae; Fl, Flemingitidae; Gy, Gyronitidae; He, Hedenstroemiidae; Ka,

Kashmiritidae; Mu, Mullericeratidae; Op, Ophiceratidae; Pn, Paranoritidae; Pr, Proptychitidae. Some genera could not be ascribed with certainty to a family, and are thus here shown at the same level as the families, with the following abbreviations: *Ki*, *Kingites*; *Kr*, *Krafficeras*; *Pa*, *Paraspidites*; *Su*, *Subacerites*; GI, Gen. Indet.

Fig. 11. Comparison of the biodiversity signal with palaeoenvironmental proxies: [A] Palynofacies of the section of Nammal Nala, modified after Hermann et al. (2011); AOM = Amorphous Organic Matter [B] Oxygen isotopes for the section of Nammal Nala, modified after Romano et al. (2013); [C] Carbonate carbon isotopes for Chiddru and Nammal (modified after Hermann et al., 2011), Amb (modified after Schneebeli-Hermann et al., 2012), and Mud and Lalung (this study); [D] Organic carbon isotopes for Chiddru and Nammal (modified after Hermann et al., 2011) and Amb (modified after Schneebeli-Hermann et al., 2012); [E] rarefied species richness curve and associated 95% confidences intervals for the Northern Indian Margin (see Fig. 5).

- A new high-resolution ammonoid biochronological zonation for the Dienerian of the Northern Indian Margin is constructed, with a total of 12 zones
- We propose to subdivide the Dienerian into three parts (early, middle and late) instead of two
- Ammonoid diversity analyses show a first moderate recovery in the early Dienerian, followed by low diversity associated with anoxic conditions and warm temperatures before the early Smithian recovery and cooling
- In addition to the younger late Smithian ammonoid extinction, mid-late Dienerian times now appear as an earlier and distinct extinction phase in the Early Triassic recovery of the clade